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Lamprospora benkertii sp. nov., and an evaluation of *Lamprospora* spp. with *seaveri*-type ascospore ornamentation

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ABSTRACT—*Lamprospora benkertii* is described as a new species based on collections from Georgia, Germany, Norway, Slovakia, and Switzerland. It is characterized by orange apothecia without a fimbriate margin, globose ascospores with a *seaveri*-type ornamentation comprising strong ridges forming a reticulum and a secondary reticulum formed by fine ridges within the meshes of the primary reticulum. The fungus infects rhizoids of *Trichostomum crispulum*. Delineation of the new species is supported by LSU and EF1α sequence analyses. *Lamprospora benkertii* is compared with other *Lamprospora* species with a *seaveri*-type or similar ascospore ornamentation: *L. ascoboloides*, *L. cailletii*, *L. dicranellae*, *L. funigera*, *L. hispanica*, *L. irregulariata*, *L. leptodictya*, *L. norvegica*, *L. paechnatzii*, *L. seaveri*. We also present an updated key for this group of species as well as a more complete description of *L. hispanica* based on our observations from several collections. New host specificity data are provided for *L. hispanica*, *L. leptodictya*, *L. norvegica*, and *L. paechnatzii*.

KEY WORDS—bryophilous *Pezizales*, cryptic diversity, host specificity, integrated taxonomy, *Pyronemataceae*

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TABLE 1. Sequences of *Lamprospora* spp. and outgroup used in the phylogenetic study.

SPECIES	HERBARIUM NUMBER	GEOGRAPHIC ORIGIN (ISO2), COLLECTOR	LSU	EF1α
L. aff. *seaveri*	PRC 4583	SK, L. Janošík	MN394609	—
	B 70 0100019	AT, M. Vega	MN394595	—
L. ascoboloides	FH KH.03.54	NO, K. Hansen	DQ220358	—
L. benkertii (holotype)	B 70 0100994	DE, J. Eckstein	MN394601	—
	TRH F-10783	NO, S. Sievertsen	MG949136	—
	B 70 0100991	CH, E. Stöckli	MN394592	MN366465
	PRC 4580	SK, L. Janošík	MN394614	—
	B 70 0100982	CH, E. Stöckli	MN394602	MN366469
	B 70 0100987	CH, M. Vega	MN394594	MN366466
	PRM 952409	SK, Z. Egertová, M. Sochor	MN400066	—
	PRM 952408	GE, Z. Egertová	MN394603	—
(as *L. norvegica*)	FH KH.03.138	NO, K. Hansen	KC012684	—
L. cailletii	B 70 0100014	CH, E. Stöckli	MN394604	—
	PRM 951726	SK, Z. Egertová, M. Sochor	MN394605	—
L. dicranellae	HBG 024467	PT, M. Vega	KY858952	—
	HBG 024470	DE, M. Vega	KY858955	—
L. hispanica	B 70 0100992	DE, J. Eckstein	MN400064	MN366467
	B 70 0100985	ES, R. Tena Lahoz	MN394593	—
	B 70 0100998	ES, M. Vega	MN394607	—
	B 70 0100979	ES, R. Martínez-Gil	MN394596	—
	B 70 0100008	ES, M. Vega	MN394598	—
	B 70 0100986	ES, M. Vega	MN394599	MN366468
	B 70 0100980	FR, M. Vega	MN394600	MN366470
	PRM 952410	HR, Z. Egertová, M. Sochor	MN394608	—
L. leptodictya	ZT Myc 61079	CH, E. Stöckli	MN394610	—
	B 70 0100009	FR, M. Vega	MN394611	—
L. norvegica	B 70 0100021	CH, E. Stöckli	MN400065	—
	TRH F-17573	NO, R. Kristiansen	MN394606	—
L. paechnatzii	B 70 0100018	DE, M. Vega, T. Richter	MN394613	—
L. seaveri (holotype)	B 70 0010018	DE, D. Benkert	MN394612	—
	B 70 0100010	DE, M. Vega	MN394597	—
Lamprospora sp.	FH KH.03.131	NO, K. Hansen	DQ220361	—
Octospora leucoloma	PRM 945804	CZ, Z. Egertová	MK569370	—

Introduction

Lamprospora De Not. exhibits a remarkable variability in ascospore ornamentation. Because it may consist of variously shaped ridges, warts, spines, tubercles, and bands, both alone and in combination, ascospore ornamentation is traditionally considered the most important character for species delimitation. In a monographic work, Benkert (1987) distinguished six basic types of ornamentation in *Lamprospora.* One type, characterized by long curved ridges, sometimes forming loops and often tapering at interjections or ends, was termed by him as *seaveri*-type (referring to *L. seaveri*).

In recent years, integrated taxonomy combining traditional morphological studies with new molecular techniques has proved a powerful tool in assessing biodiversity in all groups of organisms (e.g., Caparrós & al. 2016, Deniz & al. 2015, López-Bautista & al. 2006, Nater & al. 2017, Nedeljković & al. 2015, Zhao & al. 2019). Only recently has this approach also been applied to bryophilous *Pezizales* (Vega & al. 2017, 2019, Sochorová & al. 2019). One of the main discoveries from molecular investigations of bryophilous *Pezizales* was the very high host specificity of all investigated species. In consequence, host identity is even more important for delineating bryophilous *Pezizales* species than ascospore ornamentation (Egertová & al. 2018). This makes species reported from multiple, not closely related, hosts likely candidates for hidden diversity and due for evaluation.

Eckstein (2014) reported *Lamprospora hispanica*, one species with *seaveri*-type ascospore ornamentation, as new to Germany, citing collections on *Aloina* sp. and on the hitherto unknown host *Trichostomum crispulum* Bruch (*Pottiaceae*). Since then, we studied many more collections on both hosts and clarified that two species with similar ascospores were at hand. The aim of the present article is to describe the new species on *Trichostomum crispulum* and to compare it with other *Lamprospora* species with *seaveri*-type ascospore ornamentation.

Material and methods

Sample collection and observation

The description of macroscopic and microscopic characters is based on vital material. Microscopic structures were measured in tap water using standard light microscopy. For each collection, at least 20 ascospores and 10 other structures were measured. In all species, ascospore dimensions always include ornamentation, unless stated otherwise. Ascospore ornamentation was studied in cotton blue, and non-amyloidity checked in Lugol´s solution. Scanning electron micrographs (SEM) were taken from air-dried samples.

Herbarium acronyms follow Thiers (2019). Lists of collections are ordered alphabetically by country and from north to south within countries. Collector abbreviations include CN (Csaba Németh), DB (Dieter Benkert), EB (Emiel Brouwer), EP (Eckehard Paechnatz), ES (Elisabeth Stöckli), GE (Günter Eckstein), GM (Gianfranco Medardi), HD (Henry Dissing), JE (Jan Eckstein), LJ (Lukáš Janošík), MdlT (Margarita de la Torre), MS (Michal Sochor), MV (Marcel Vega), RK (Roy Kristiansen), RMG (Rubén Martínez-Gil), RTL (Raúl Tena Lahoz), SS (Sigmund Sivertsen), TR (Torsten Richter), ZE (Zuzana Egertová).

DNA extraction, PCR amplification, sequencing

DNA was extracted from fresh, dried, or CTAB-stored apothecia using the CTAB method (Doyle & Doyle 1987) or the Zymo Research Fungal/Bacterial kit. Amplification was carried out for the 28S subunit of ribosomal DNA (LSU) using primers LR0R and LR6 (Vilgalys & Hester 1990) and for the translation elongation factor-1alpha (EF1α) with primers EF1-983F and EF1–1567R (Rehner & Buckley 2005). PCR was performed with Kapa polymerase, following a standard protocol with 37 cycles and annealing temperature of 56°C. The PCR products were purified by precipitation with polyethylene glycol (10% PEG 6000 and 1.25M NaCl in the precipitation mixture) and sequenced in both directions using the Sanger method (Macrogen Europe, The Netherlands and Sequencing laboratory of the Faculty of Science, Charles University, Prague, Czech Republic).

Phylogenetic analysis

LSU rDNA sequences analyzed included nine sequences of *L. benkertii*, eight of *L. hispanica*, one or two of other *Lamprospora* species with similar ascospore ornamentation, and *Octospora leucoloma* Hedw. as outgroup. Additionally, EF1α was analyzed in selected collections of *L. benkertii* and *L. hispanica*. Along with sequences newly generated in this study, relevant data from the GenBank database were used (https://blast.ncbi.nlm.nih.gov; sequences originate from Perry & al. 2007, Hansen & al. 2013, Vega & al. 2017, and Egertová & al. 2018). Sequences were assembled, edited, and aligned using GENEIOUS (ver. 7.1.7., Biomatters). Bayesian phylogeny inference (BI) was computed in MRBAYES (ver. 3.2.4, Ronquist & al. 2012) using the GTR+I+G substitution model, as determined by AICc in JMODELTEST (ver. 2.1.4, Darriba & al. 2012). The analysis was run for 10 million generations in two independent runs, sampling every 1000th generation and excluding the first 25% of generations as burn-in. Sequences and GenBank accession numbers used in the phylogenetic analysis are listed in TABLE 1.

Taxonomy

Lamprospora benkertii Eckstein, M. Vega, Sochorová & Janošík, **sp. nov.** FIGS 1–4

MB 831135

Differs from similar *Lamprospora* species by its apothecia without a fimbriate margin, globose ascospores with an alveolate reticulum formed by strong ridges, and infections located on rhizoids of *Trichostomum crispulum*.

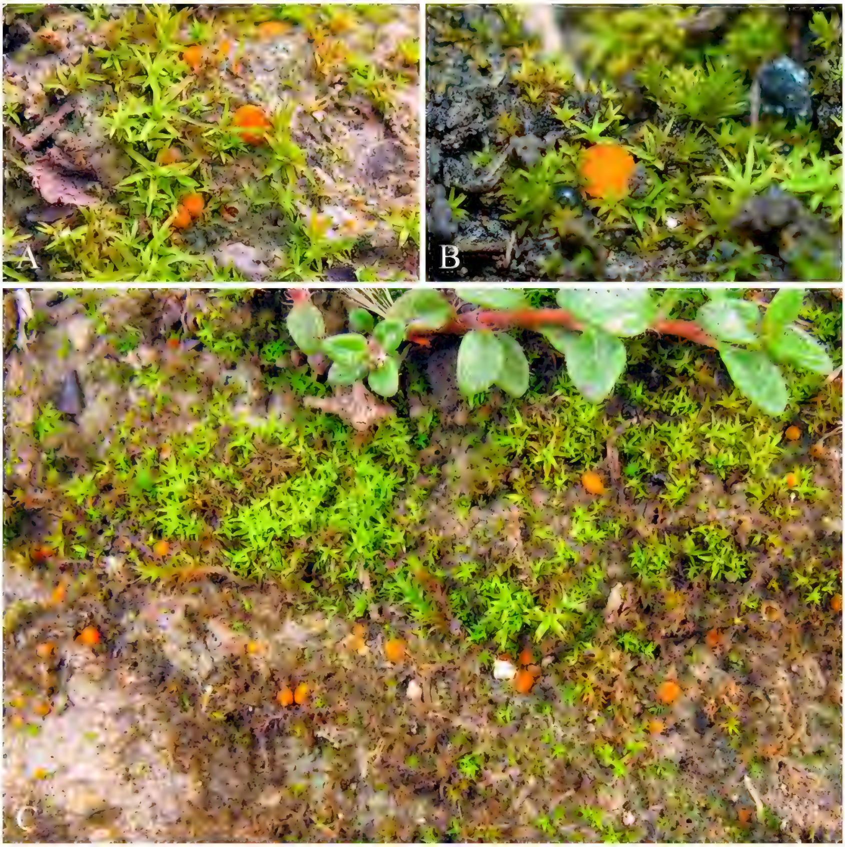

Fig. 1. *Lamprospora benkertii* (A, C. holotype; B. B 70 0100991). Apothecia on soil between shoots of *Trichostomum crispulum*.

Type: Germany, Saxony-Anhalt, Western slope of Spielberger Höhe 1 km ENE Spielberg, 51.3247°N 11.5992°E, 220 m a.s.l., on loamy-calcareous soil with *Trichostomum crispulum*, *Didymodon fallax*, and *Ephemerum recurvifolium*, 12.VIII.2011, JE22084 (**Holotype**, B 70 0100994).

Etymology: honoring Dieter Benkert for his meritorious service in the taxonomy of bryophilous *Pezizales*

Apothecia gregarious on soil between shoots of *Trichostomum*, (0.2–)0.4–1 (–1.5) mm in diameter, first spherical, becoming cup-shaped, finally discoid with a flat hymenium, sessile, with few hyaline and flexuous anchoring hyphae at the base; margin inconspicuous; hymenium orange to bright orange, outer surface slightly paler.

Asci 180–250(–325) × 18–28 µm, cylindrical to slightly club-shaped, 8-spored, unitunicate, operculate, inamyloid, arising from croziers.

Ascospores uniseriate, hyaline, thin-walled, globose, 13–16.5 µm in diameter (ornamentation included) or 12–14.5 µm without ornamentation, always with a lipid drop, 8–10(–11) µm diameter; ornamentation of the *seaveri*-type consisting of curved ridges approximately 0.8–1.2(–1.6) µm wide and 0.8–1.2 µm high, forming a coarse alveolate reticulum with 4–8 meshes across ascospore diameter, meshes fairly variable and always with a thin secondary net of fine ridges, ridges rarely with loops, sometimes circling the ascospore and rarely ending blind, anastomosing ridges often tapered towards intersection, ornamentation cyanophilous, quickly dissolving in potassium hydroxide (10% KOH).

Paraphyses filiform, straight, pluriseptate, rarely forked and only in lower third, gradually widening from 2.5–3 µm in lower third to 4–6(–8) µm at tip, terminal cell (30–)45–85(–100) µm long, with distinctive carotenoid pigment turning cyan to olivaceous in Lugol's solution, and numerous vacuolar bodies, size ≤4 µm.

Subhymenium consisting of thin-walled, variously shaped, hyaline cells 2.5–6 µm broad, merged with the medullary excipulum; Medullary excipulum about 60–90 µm thick, comprising thin-walled, variously shaped cells forming a textura intricata; Ectal excipulum ca. 40–55 µm thick, comprising thick-walled globose, subglobose to subangular cells (textura subglobulosa), 6–20 × 5–18 µm, cell wall ≤3 µm thick; Margo of parallel hyphae with thick-walled end cells 20–50 × 4–10 µm not (or minimally) protruding over the hymenium (textura prismatica-porrecta).

Infections located on rhizoids of *Trichostomum crispulum*, consisting of mostly 1-celled ellipsoid appressoria, 20–30 × 10–12 µm, sometimes with a somewhat enlarged adjacent cell, initially free, becoming completely covered with anchoring hyphae; infection peg ca. 1 µm wide, surrounded by a tube of rhizoid cell-wall material, forming intracellular haustoria; Penetration point surrounded by a circular thickening of the rhizoid wall; haustoria often ramified with irregular shape and without cross walls, not growing through rhizoid walls; growth modifications with inflated cells and more cross walls

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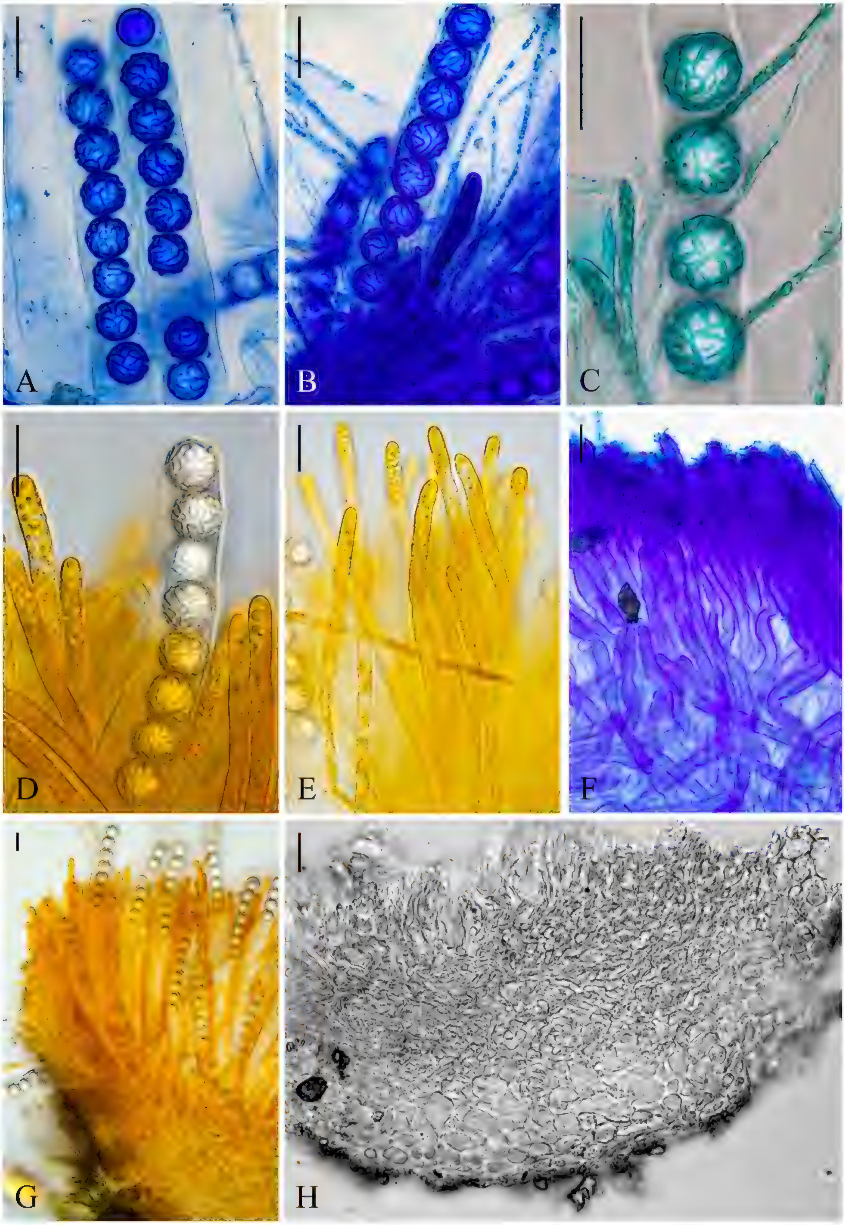
Fig. 2. *Lamprospora benkertii* (A, F, H. holotype; B. B 70 0100987; C. PRC 4580; D, E, G. PRC 4601). A–C. Ascospores stained with cotton blue. D. Ascospores and paraphyses in water. E. Upper part of paraphyses in water. F. Marginal hyphae of an apothecium seen from outside



stained with cotton blue. G. Cross section of a vital apothecium showing margin, excipulum, and hymenium. H. Cross section of a dried apothecium showing subhymenium, medullary, and ectal excipulum. Scale bars = 20 µm.

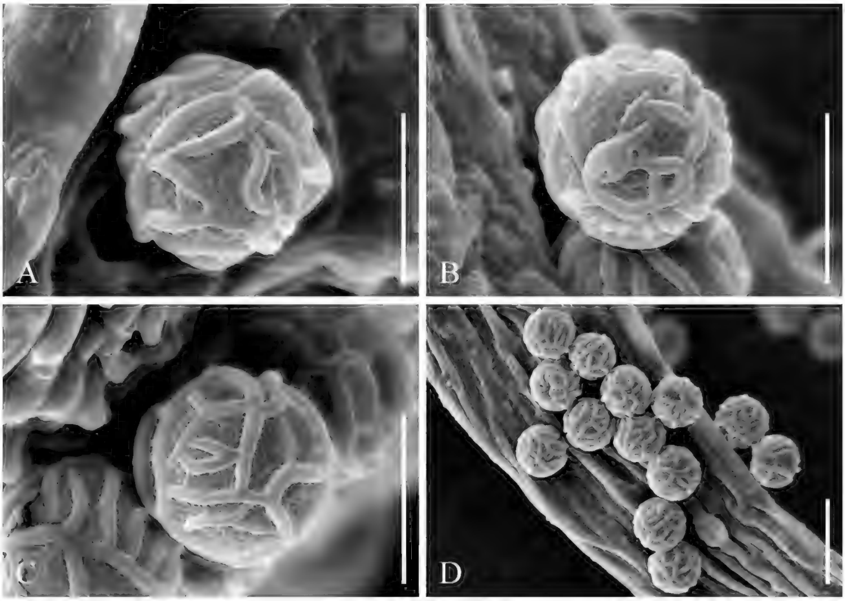


Fig. 3. *Lamprospora benkertii* (A–B. holotype; C–D. B 70 0100987). Ascospores (SEM). Scale bars: A–C. = 10 µm; D. = 20 µm.

than normal sometimes observed on infected and adjacent rhizoid cells; HOST not weakened discernibly by the infection.

Ecology & distribution—On soil in open situations like grassland, or along tracks and paths together with bryophytes including, apart from the host, *Aloina* spp., *Didymodon fallax, D. acutus, Ephemerum recurvifolium,* and *Weissia longifolia.* Known from Georgia, Germany, Norway, Slovakia, and Switzerland.

Additional specimens examined—**GEORGIA. Racha-Lechkhumi and Kvemo Svaneti, Racha mountains,** 5 km E of Shovi, 42.6911°N 43.7317°E, 2240 m a.s.l., 27.VI.2014 ZE (PRM 952408). **GERMANY. Saxony-Anhalt, NE Grockstädt,** 51.3331°N 11.5931E, 220 m a.s.l., on calcareous soil in dry grassland, 21.VIII.2017 JE51316 (B 70 0100984); **2.35 km NNE Reinsdorf,** 51.3128°N 11.6183°E, 195 m a.s.l., on south-facing slopes of loess-soil with *Trichostomum crispulum,* 11.X.2011 JE22454 (B 70 0100996). **NORWAY. Nordland, Saltdal,** Junkerdalen, Gammelveien innenf. bommen, 120 m a.s.l., between mosses on track, 31.VIII.1988 SS88-78 (TRH F-10783 as *Lamprospora* cf. *ascoboloides*); 29.VIII.1998 HD&SS98-14 (TRH F-10639 as *Lamprospora ascoboloides*). **SLOVAKIA. Žilina, Súľov-Hradná,** 49.1576°N 18.5808°E, 425 m a.s.l., margin of a forest way, 20.VIII.2016, ZE (PRM 952409); **Trenčín, Trenčín,** 48.8876°N 18.0610°E, 220 m a.s.l., between mosses on the margin of a small forest path,

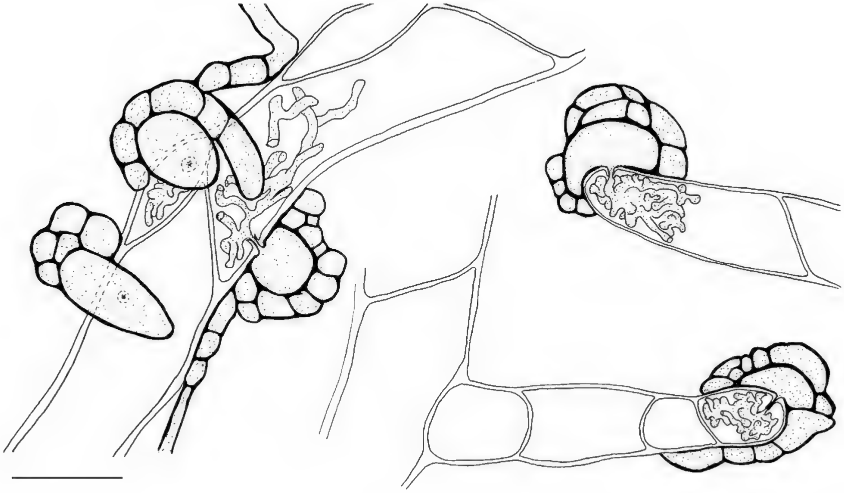


Fig. 4. *Lamprospora benkertii* (holotype). Several infectious structures in optical section on rhizoids of *Trichostomum crispulum*; fungal cells dotted. Scale bar = 20 µm.

10.XII.2014 LJ (PRC 4579); **Beckovské Skalice,** 48.7744°N 17.8944°E, 220 m a.s.l., on path in grassland, 07.X.2014 LJ (PRC 4580); 27.X.2019 LJ (PRC 4601). **SWITZERLAND. Bern, Gasteretal,** 46.4672°N 7.6611°E, 1350 m a.s.l., on soil, 30.IX.2016 ES (B 70 0100991); **Kandersteg,** 46.4744°N 7.6572°E, 1240 m a.s.l., on soil in grazing land, 25.VIII.2018 MV180825-2 (B 70 0100987); 46.4447°N 7.7225°E, 1580 m a.s.l., on soil in grazing land, 04.X.2013 ES (B 70 0100982).

Phylogenetic analysis—*Lamprospora benkertii* forms a well-supported clade with very little polymorphism among individual collections (Fig 5). In LSU, five collections are fully identical (MN394601 – holotype, MN400066, MN394592, MN394614, and MN394602), with three others differing only in a single nucleotide (MG949136, MN394603 and KC012684 — published as *L. norvegica* by Hansen & al. 2013) and one other in another single nucleotide (MN394594). *Lamprospora paechnatzii* was identified as the closest relative of *L. benkertii; L. hispanica,* which is morphologically very similar to *L. benkertii,* differs strongly both in LSU and EF1α (data not shown). A similar phenomenon was also observed in *L. seaveri* sensu lato, which was described as associated with *Ceratodon purpureus* and *Bryum* sp. (Benkert 1987); however, collections from these two hosts form independent lineages.

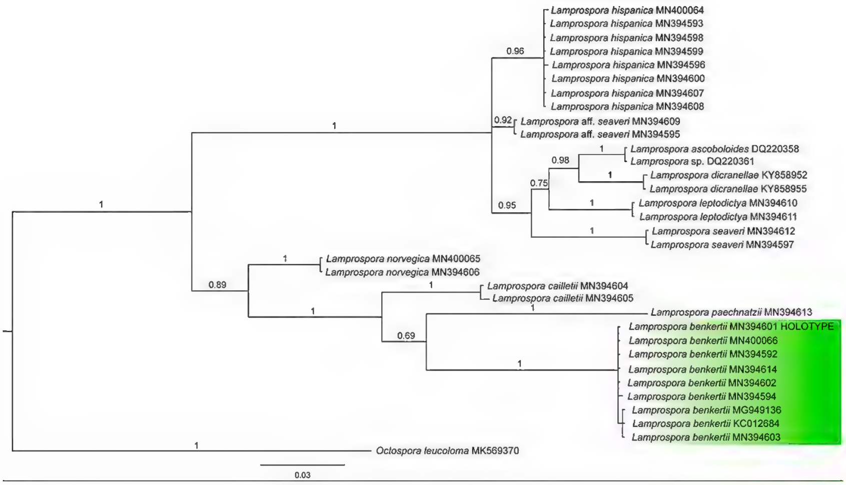

Lamprospora hispanica MN400064
Lamprospora hispanica MN394593
Lamprospora hispanica MN394598
Lamprospora hispanica MN394599
Lamprospora hispanica MN394596
Lamprospora hispanica MN394600
Lamprospora hispanica MN394607
Lamprospora hispanica MN394608
Lamprospora aff. seaveri MN394609
Lamprospora aff. seaveri MN394595
Lamprospora ascoboloides DQ220358
Lamprospora sp. DQ220361
Lamprospora dicranellae KY858952
Lamprospora dicranellae KY858955
Lamprospora leptodictya MN394610
Lamprospora leptodictya MN394611
Lamprospora seaveri MN394612
Lamprospora seaveri MN394597
Lamprospora norvegica MN400065
Lamprospora norvegica MN394606
Lamprospora cailletii MN394604
Lamprospora cailletii MN394605
Lamprospora paechnatzii MN394613
Lamprospora benkertii MN394601 HOLOTYPE
Lamprospora benkertii MN400066
Lamprospora benkertii MN394592
Lamprospora benkertii MN394614
Lamprospora benkertii MN394602
Lamprospora benkertii MN394594
Lamprospora benkertii MG949136
Lamprospora benkertii KC012684
Lamprospora benkertii MN394603
Octospora leucoloma MK569370
0.96
0.92
0.98
0.75
0.95
0.89
0.69
1
0.03

Fig. 5. Bayesian phylogram of *Lamprospora* spp. based on LSU rRNA sequences, with *Octospora leucoloma* as outgroup. Bayesian posterior probabilities are shown above branches.

Comments—*Trichostomum crispulum*, the host of the new *L. benkertii*, is not known as a host of other bryophilous *Pezizales*. It has a circumpolar southern-temperate distribution with occurrences in Europe, Asia Minor, Siberia, East Asia, New Guinea, Macaronesia, North and Central Africa, Newfoundland, and Central America (Smith 2004).

In his main contribution to the taxonomy of *Lamprospora*, Benkert (1987) listed six species with *seaveri*-type ascospore ornamentation: *L. cailletii*, *L. hispanica* and *L. seaveri*, as well as *L. ascoboloides*, *L. leptodictya* and *L. paechnatzii*. The first three species were assigned to the subtype '*seaveri*,' characterized by anastomosing ridges forming an alveolate reticulum, and the latter three to the subtype '*paechnatzii*', delineated by only partly anastomosing ridges not forming a reticulum. Subsequently, another species, *L. norvegica*, was also described with *seaveri*-type ornamentation (Benkert & al. 1991).

Two little known species, *L. irregulariata* from India and *L. funigera* from Australia, also must be considered in this context. Additionally, we include *L. dicranellae* Benkert in this discussion, because in the past it has frequently been mistaken for *L. ascoboloides*. We discuss these species in alphabetical order below with delineations based on our own observations except for *L. funigera* and *L. irregulariata*.

Lamprospora ascoboloides Seaver, Mycologia 6: 10. 1914.

Based on collections from the US states Connecticut, New York, and Virginia, *L. ascoboloides* is characterized by globose ascospores 13–15(–17) µm in diameter [12–14 µm in Benkert (1987) and (14–)16–18 µm incl. ornamentation in Wang & Kimbrough (1992)], ornamented by curved ridges 1–2 µm wide and 1–1.5(–2) µm high that often end bluntly and do not (or hardly) form a rudimentary reticulum (Seaver 1914, Benkert 1987, Wang & Kimbrough 1992). Furthermore, the ornamentation lacks warts. Our study of the NY type material revealed a dicranelloid moss as the host. (probably *Dicranella heteromalla*, but with juvenile shoots too small for certain identification). Notably, the infection induces spherical galls 40–80 µm in diameter on the rhizoids. These rhizoid galls are completely covered with a layer of hyphae. *L. ascoboloides* differs from *L. benkertii* in broader ridges and the host.

The name *L. ascoboloides* was later applied many times to collections with strong, curved ridges as ascospore ornamentation, but critical studies of these specimens always led to other identifications. For instance, *L. ascoboloides* in reports by Caillet & Moyne (1980) was later re-determined by Benkert (1987) as *L. dicranellae*. The description and illustrations of '*L. ascoboloides*' by Schumacher (1993) also clearly show *L. dicranellae*. Our revision of *L. ascoboloides* specimens in TRH indicated mostly *L. dicranellae* or rarely *L. arvensis* (Velen.) Svrček as well as several yet undescribed species. We also revised a specimen from K (listed in Medardi 2006) to *L. dicranellae*. We also studied two collections sequenced by Perry & al. (2007, GenBank accession numbers DQ220358 and DQ220361) that also have *L. dicranellae*-like ascospores, but their sequences do not cluster with other *L. dicranellae* samples (Vega & al. 2017), clearly indicating that further study is needed. *Dicranella* species were not found as hosts in any of these cases. Medardi (2005) reported *L. ascoboloides* from Italy accompanied by *Dicranella*, *Ditrichum*, *Riccia*, and *Anthoceros*. Unfortunately, our investigation of MCVE 15993 resulted in no unambiguous observation of the infection but the host is most likely *Dicranella* or *Ditrichum*. Therefore, the specimen could represent *L. ascoboloides* but without definite identification of the host, its identity remains unclear. Hopefully, future collections from both North America and Europe will shed light on this subject.

SPECIMENS EXAMINED (for revised specimens see *L. dicranellae*)—ITALY. **LOMBARDY, Calvagese**, Brescia, 300 m a.s.l., with *Dicranella*, *Ditrichum*, *Riccia*, and *Anthoceros*, 09.VI.2001 GM (MCVE 15993 as *L. ascoboloides*).

Lamprospora cailletii Benkert, Z. Mykol. 53: 211. 1987.

Based on a collection from the French Alps, *L. cailletii* is characterized by 1–2 mm diameter yellow-orange apothecia with small fimbriate margins, globose ascospores (14)15–16.5(17) µm, ornamented by curved ridges 0.8–1.5 µm wide and high forming a reticulum and additional warts, and *Tortella tortuosa* as host (illustrations in Kristiansen 2006, Stöckli 2016). The additional warts are sometimes difficult to see, and then the ascospore ornamentation looks very similar to that of *L. benkertii*. It further differs from *L. benkertii* by the small apothecial margins, slightly larger ascospores, lack of secondary reticulum, and identity of the host.

Formerly *L. cailletii* was only rarely reported from France and Germany (Benkert 1987), Norway (Kristiansen 2006), and Switzerland (Stöckli 2016). Newly, we report it from Slovakia. We doubt that the report on *Ditrichum flexicaule* (Schwägr.) Hampe by Schumacher (1993) from France is actually from this species.

Selected specimens examined—**SLOVAKIA. Žilina, Terchová,** 1870 m SSW of St. Cyril and Metod´s church, Malá Fatra NP, 49.2417°N 19.0261°E, 935 m a.s.l., on soil with *Tortella tortuosa*, 29.X.2016, ZE & MS (PRM 951726). **SWITZERLAND. Jura, Montfaucon,** 47.2755°N 7.0793°E, 930 m a.s.l., host *Tortella tortuosa*, 18.X.2015 ES (B 70 0100014).

Lamprospora dicranellae Benkert, Z. Mykol. 53: 217. 1987.

Based on collections from the Czech Republic, Germany, Denmark, France, Norway, and Sweden, *L. dicranellae* is characterized by orange apothecia 1–3 mm in diameter with conspicuous fimbriate margins, globose ascospores (14)15–16.5(17) µm, ornamented by curved ridges 1–2 µm wide and high forming a reticulum and additional warts (Fig. 7A). The host is not *Dicranella* as assumed in the protologue but *Ditrichum heteromallum* and *D. pusillum* (Eckstein & al. 2014, Vega & al. 2017). *L. dicranellae* differs from *L. benkertii* by its larger apothecia with conspicuous fimbriate margins, the existence of many prominent warts in addition to curved ridges on the ascospore surface, and identity of the host.

Lamprospora dicranellae is a relatively widespread species with further occurrences not mentioned in the protologue, e.g., in Austria and on the Canary Islands and Madeira (Korf & Zhuang 1991) and in Great Britain (Yao & Spooner 1995), the Netherlands (Brouwer 1999), Spain (Rubio & al. 2002), and the USA (Wang & Kimbrough 1992).

SELECTED SPECIMENS EXAMINED—**AUSTRIA. CARINTHIA, Nockberge,** above Zechneralm, 46.9494°N 13.7576°E, 1970 m a.s.l., 10.VIII.2015 JE42349 (B 70 0100988). **SALZBURG, Uttendorf, Staubachtal,** on sandy soil near mosses, 18.VIII.2005 GM (K[M] 138534 as *L. ascoboloides*). **GERMANY. THURINGIA, Eisenach,** S Wartburg, 50.9581°N 10.2998°E, 280 m a.s.l., host *Ditrichum* sp., 27.IX.2017 JE51668 (B 70 0100989). **NORWAY. OPPLAND, Vang,** Tyinholmen, 1100 m a.s.l., host *Ditrichum* cf. *pusillum*, 23.VIII.1986 RK (TRH F-9757 as *L. ascoboloides*).

Lamprospora funigera McLennan & Cookson, Proc. Roy. Soc. Victoria 38: 70. 1926.

Based on two collections from the state Victoria in Australia, *L. funigera* is characterized by apothecia 1–3 mm in diameter with well-developed fimbriate margins, globose ascospores 12–13 µm in diameter, ornamented by curved ridges forming a reticulum. The host is unknown. It differs from *L. benkertii* in larger apothecia with a conspicuous fimbriate margin and smaller ascospores. So far *L. funigera* is only known from the type specimen (McLennan & Cookson 1926).

Lamprospora hispanica Benkert, Z. Mykol. 53: 227. 1987. FIGS 6, 7B

This species is based on one collection from Spain. Studying the holotype in MA we found some differences between the original description and our observations later confirmed by many identical collections from different countries. Because of the partly incorrect original description, we provide here a more complete description based on our own observations (FIG. 6, 7B):

APOTHECIA gregarious, occasionally packed, on soil between shoots of *Aloina*, 1–2(3) mm in diameter, at first spherical, becoming cup-shaped, finally thick and discoid with a flat hymenium, sessile, with hyaline and flexuous anchoring hyphae; MARGIN conspicuous, fimbriate to shaggy; HYMENIUM varying from pale orange to orange, margin and outer surface paler.

ASCI 250–450 × 20–28 µm, cylindrical, 8-spored, unitunicate, operculate, inamyloid, bifurcate at the base, arising from croziers.

ASCOSPORES subglobose, hyaline, uniseriate, 16–19(22) × 15–18(20) µm (ornamentation included), Q: 1.03–1.06(1.1), always with a lipid drop (10)11–13 µm in diameter; ORNAMENTATION consisting of an alveolate reticulum of the *seaveri*-type, with 5–8(10) meshes across ascospore diameter, with the net's density varying considerably between collections, meshes fairly variable, often with lower and thinner ridges that may form a secondary net, ascospore surface slightly roughened with occasionally minute stains, main ridges approximately 0.8–1.0 µm wide and 0.6–0.8(1) µm high, sometimes with loops, anastomosing ridges not or rarely tapering at interjections.

PARAPHYSES filiform, straight, pluriseptate, branched at the base, gradually enlarging towards the apex, terminal cell 50–120 × 4–8 µm, distinctive carotenoid pigment turning cyan to olivaceous in Lugol's solution, at times in lipid bodies, numerous vacuolar bodies ≤4 µm in size.

MEDULLARY EXCIPULUM textura intricata; ECTAL EXCIPULUM textura prismatica-angularis; MARGO textura prismatica-porrecta, cells 36–120 × 10–30 µm.

INFECTION on strong rhizoids of *Aloina aloides* (Koch ex Schultz) Kindb. or *Aloina ambigua* (Bruch & Schimp.) Limpr. consisting of appressoria, infection peg and haustoria; APPRESSORIA clearly differentiated, attached to the rhizoid becoming completely covered which anchoring hyphae, 30–60(75) × 25–35(50) µm in side view, mostly 2-septate, often multiple infection pegs originating from one appressorium.

ECOLOGY & DISTRIBUTION—*L. hispanica* occurs on soil in open and mostly warm habitats such as in dry grassland, in cemeteries, or along paths. It does not seem to be rare in Spain (Ortega & Vizoso 1991, Martínez-Gil & Caballero 2015). Additional collections have been made in Croatia, Cyprus, France, Germany, Hungary, Portugal, and The Netherlands, with distribution seemingly centered in the Mediterranean region with scattered occurrences further north in the temperate zone. Given its known distribution, it is possible that the species might occur in all Central and Southern European countries.

Lamprospora hispanica differs from *L. benkertii* by its larger apothecia with conspicuous fimbriate margins, its slightly subglobose ascospores with more uniformly wide ridges forming a denser net, its much larger appressoria, and the identity of its host.

SELECTED SPECIMENS EXAMINED—**CROATIA. KARLOVAC, Modruš** rest area, 45.1301°N 15.2483°E, 500 m a.s.l., on soil with *Aloina* sp., 20.XI.2016 ZE (PRM 952410). **CYPRUS. PAPHOS, Peiya**, 34.8936°N 32.3794°E, 440 m a.s.l., on soil layer on stone wall, host *Aloina* sp., 28.II.2019 MV190228-07 (B 70 0100981). **FRANCE. GIRONDE, Cenon**, Parc Palmer, 44.8611°N 0.5261°W, 55 m a.s.l., slope beside a path, host *Aloina ambigua*, 06.IV.2018 MV180406-01 (B 70 0100978). **HAUTE GARONNE, Toulouse**, cemetery of Terre-Cabade, 43.6067°N 1.4603°E, 170 m a.s.l., on soil between graves, host *Aloina ambigua*, 14.II.2017 MV170214-03 (B 70 0100980). **GERMANY. HESSE, Werra valley**, Weinberg W Jestädt, 51.2188°N 9.9955°E, 180 m a.s.l., on soil in dry grassland, host *Aloina ambigua*, 18.I.2014 JE34631 (B 70 0100990); **LOWER SAXONY, N Tettenborn**, 51.5716°N 10.5534°E, 320 m a.s.l., in an old quarry on loamy soil with

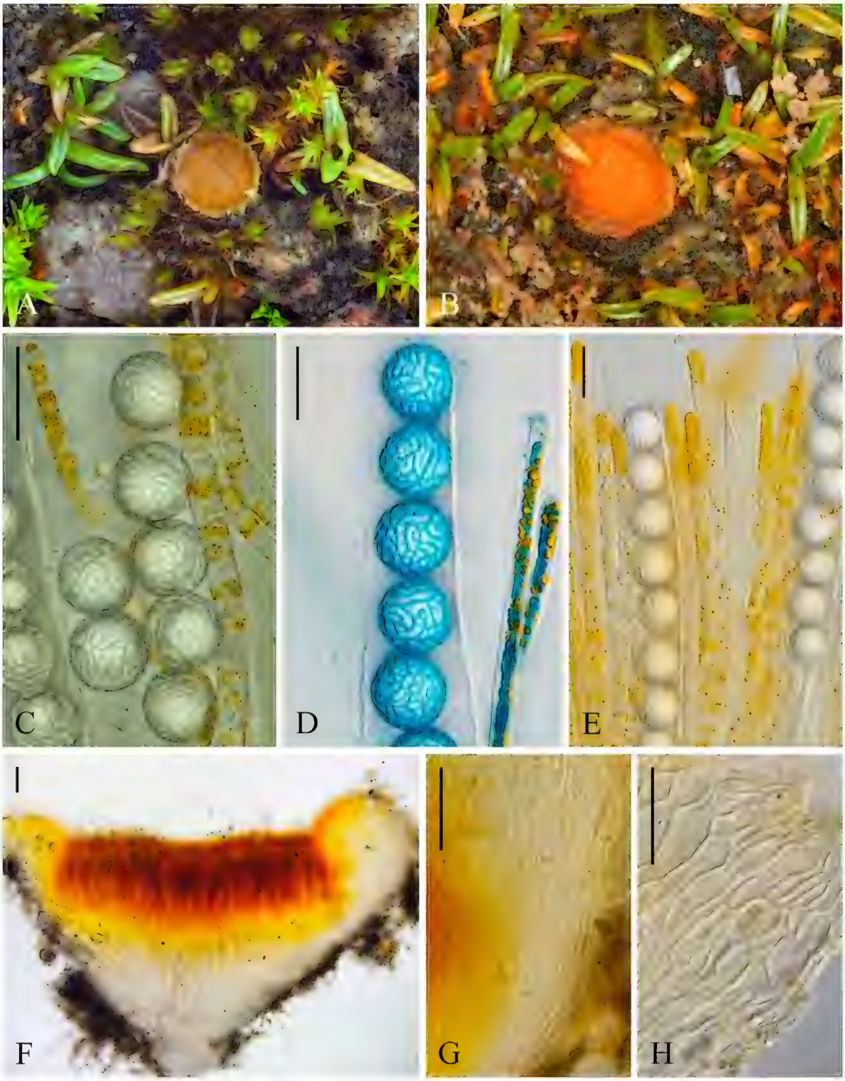


Fig. 6. *Lamprospora hispanica* (A. B 70 0100990; B–H. B 70 0100980). A, B. Apothecia on soil with shoots of *Aloina* sp. C. Ascospores in water. D. Ascospores stained with cotton blue. E. Paraphyses and asci in water. F. Cross section of an apothecium. G. Medullary excipulum next to the hymenium. H. Cross section of upper margin of an apothecium. Scale bars: C–E. = 20 µm; F–H. = 100 µm.

gypsum, host *Aloina aloides*, 22.XI.2016 JE49371 (B 70 0100992). **HUNGARY. Fejér, Vèrtes Mts.**, Csàkvòr, Szòlò-Kö. 47.3804°N 18.4374°E, 200 m a.s.l., host *Aloina ambigua*, 05.III.2016 CN7751 (private herbarium CN). **PORTUGAL. Lisboa, Cémiterio do Alto de São João,** 38.7303°N 9.1206°W, 70 m a.s.l., on soil between graves, host *Aloina ambigua*, 25.I.2014 MV140125-13 (B 70 0100995). **SPAIN. Aragón, Teruel,** Calle Bajo Los Arcos, 40.3458°N 1.1058°W, on soil in front of a house, host *Aloina ambigua*, 30.IX.2015 RTL15093001 (B 70 0100985); **La Rioja, Logroño,** Parque La Grajera, 42.4464°N 2.5078°W, 440 m a.s.l., on soil between trees of *Populus* sp., 05.XII.2014 RMG (B 70 0100979); **Madrid, Aranjuez,** 06.III.1975 MdlT (MA-Fungi 2359, holotype); **Mallorca, Inca,** Parque Llubi Torradas, 39.7064°N 2.9967°E, 80 m a.s.l., below a tree, host *Aloina* sp., 01.XII.2017 MV171201-06 (B 70 0100983); **Palma de Mallorca,** Placa del Rentadors, 39.5694°N 2.6389°E, 10 m a.s.l., amenity land, host *Aloina ambigua*, 22.I.2017 MV170122-03 (B 70 0100986); **País Vasco, Parque Ribera,** host *Aloina ambigua*, 23.I.2016 MV160123-02 (B 70 0100008); **Urkiola,** Calle Barrio de Urkiola, 43.1003°N 2.6447°W, 730 m a.s.l., bank alongside the road, host *Aloina aloides*, 19.VI.2018 MV180619-01 (B 70 0100998). **THE NETHERLANDS. Zeeland, Oosterschelde-dam,** south of Burgh-Haamstede, on Neeltje-Jans near Expo, 1 m a.s.l., on sandy recreation area, partly covered with gravel, host *Aloina ambigua*, 31.XII.2008 EB270 (private herbarium EB).

Lamprospora irregulariata K.B. Khare & V.P. Tewari, Mycologia 70: 885. 1978.

Based on a collection from Mussoorie in the state Uttarakhand in northern India, *L. irregulariata* is characterized by apothecia 2–3 mm in diameter, a yellow-white hymenium, globose ascospores 13–16 µm, ornamented by thick curved ridges forming an incomplete reticulum. The host is not known. The yellow white color of the hymenium set this species clearly apart from *L. benkertii* and even raises doubts in its affiliation to the genus *Lamprospora*. It is known only from the type (Khare & Tewari 1978).

Lamprospora leptodictya Dissing, Mycologia 73: 263. 1981.

Based on a collection from Greenland, *L. leptodictya* is characterized by apothecia 0.8–1.8 mm in diameter with conspicuous fimbriate margins, an orange hymenium, subglobose ascospores, 15–17 × 13–15.5 µm, Q ≤1.1, ornamented with curved, often blunt ending and tapering and only partly anastomosing ridges 0.5–0.9 µm wide and 0.5 µm high (Fig. 7C), and its host *Aongstroemia longipes* (Sommerf.) Bruch & Schimp. It differs from *L. benkertii* by its subglobose ascospores, smaller ridges not forming a reticulum, and its host.

Dissing notes *A. longipes* and *Bryum* sp. as accompanying bryophytes. Benkert (1987) studied a later collection from the type locality and suspected

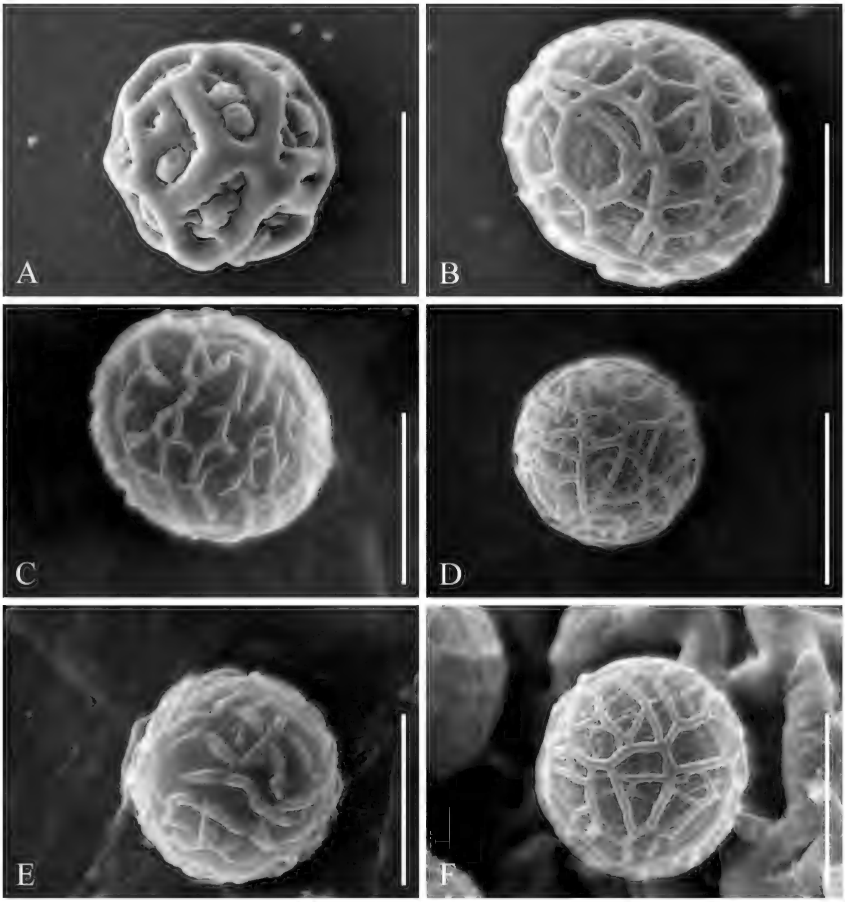


Fig. 7. SEM of ascospores of species similar to *Lamprospora benkertii*. A. *L. dicranellae* (B 70 0100989); B. *L. hispanica* (B 70 0100998); C. *L. leptodictya* (B 70 0100009); D. *L. norvegica* (B 70 0100021); E. *L. paechnatzii* (private herbarium TR 22VI2014, s.n.); F. *L. seaveri* (B 70 0010018, holotype). Scale bars = 10 µm.

Bryum sp. as host but could not actually find the infection. In specimens from the French and Swiss Alps we confirmed *A. longipes* as the host. The ornamentation is similar to that of *L. paechnatzii* with often short and blunt ending ridges not or hardly forming a reticulate pattern.

Based on the few reports and the distribution of the host moss, *L. leptodictya* is an arctic-alpine species, known from Greenland (Dissing 1981), Norway (Schumacher 1993), France (Van Vooren 2017), and Switzerland.

Specimen examined—**FRANCE. Savoy, Bonneval-sur-Arc,** Ruisseau de Céma,45.4250°N 7.0419°E, 2740 m a.s.l., host *Aongstroemia longipes*, 26.VIII.2015 MV20150826-01 (B 70 0100009). **SWITZERLAND. Bern, Guttannen,** Oberaarstausee, 46.5474°N 8.2769°E, 2306 m a.s.l., host *Aongstroemia longipes*, 18.VIII.2014 ES (ZT Myc 61079).

Lamprospora norvegica Benkert, Aas & R. Kristiansen, Z. Mykol. 57: 196. 1991.

Based on collections from mainland Norway, *L. norvegica* is characterized by apothecia 0.7–1.0(1.5) mm in diameter with conspicuous fimbriate margins, an orange hymenium, globose to slightly subglobose ascospores, 13–14 × 12–13 µm (Q ≤1.08), ornamented with curved ridges 0.3–0.7 µm wide and 0.5 µm high forming a reticulum (Fig. 7D). It differs from *L. benkertii* by slightly subglobose ascospores, smaller ridges, and host.

Benkert & al. (1991) suspected *Pohlia filum* as host but could not actually prove this. We studied collections from Norway and Switzerland and in two collections, we could identify *Ditrichum pusillum* (Hedw.) Hampe as host. The infection causes the swelling of infected rhizoid cells forming spherical galls.

Lamprospora norvegica is known from Norway (Benkert & al. 1991), Svalbard (Schumacher 1993), and Switzerland.

Specimens examined—**NORWAY. Buskerod, Hol,** Raggsteindalsvegen, 60.6666°N 7.8147°E, 1000 m a.s.l., host *Ditrichum pusillum*, 01.VIII.2015 RK (TRH F-17572). **Hordaland, Ulvik,** Finse, near Finse railway station, 60.60°N 7.50°E, 1300 m a.s.l., host probably *Ditrichum pusillum*, 24.VIII.2008 RK29/06 (TRH F-17573). **SWITZERLAND. Bern, Gadmen,** Steingletscher, 46.7233°N 8.4340°E, 1930 m a.s.l., host *Ditrichum pusillum*, 17.VII.2014 ES (B 70 0100021).

Lamprospora paechnatzii Benkert, Z. Mykol. 53: 237. 1987.

Based on a collection from the German lowlands *L. paechnatzii* is characterized by apothecia 1–2 mm in diameter, with low but conspicuous fimbriate margins, a yellow to yellowish orange hymenium, globose ascospores (14–16 µm in diameter) ornamented with curved often blunt ending and tapering ridges 0.3–0.8 µm wide and high, short and often S-shaped, rarely anastomosing and not forming a reticulum (Fig. 7E), and the host *Bryum archangelicum* Bruch & Schimp. It differs from *L. benkertii* by smaller ridges not forming a reticulum and the host.

Benkert reports *Bryum* sp. as the host; but our examination of the type specimen revealed *B. archangelicum* as the host moss.

Lamprospora paechnatzii is known from Germany and the Czech Republic (Benkert (1987) and Spain (Rubio & al. 2002).

Specimens examined—GERMANY. **Brandenburg, Bernau,** Kiesgrube Schwanebeck-Alpenberge, host *Bryum archangelicum*, VII.1978 EP (B 70 0010013, holotype); **Mecklenburg-Western Pomerania, Lützow,** gravel pit N Pokrent, host *Bryum* sp., 22.VI.2014 TR (private herbarium TR); host *Bryum* sp., 05.VIII.2014 MV140805-04 (B 70 0100018).

Lamprospora seaveri Benkert, Z. Mykol. 53: 241. 1987.

Based on many collections from Central and Northern Europe, *L. seaveri* is characterized by orange apothecia 1–4 mm in diameter with conspicuous fimbriate margins, an orange hymenium, globose ascospores 14–16 µm in diameter with an ornamentation consisting of fine ridges 0.3–0.8 µm wide and high forming a reticulum, often with a secondary reticulum within the meshes (Fig. 7F), and the host *Ceratodon purpureus*. It differs from *L. benkertii* by its larger apothecia with a conspicuous margin, smaller ridges, and host identity.

Benkert (1987) mentions the misapplication of the name *Lamprospora laetirubra* (Cooke) Lagarde for this species; the type of the basionym *Peziza laetirubra* Cooke is conspecific with *Pulvinula cinnabarina* (Fuckel) Boud. Although the designated holotype of *L. seaveri* has *Ceratodon purpureus* as host, Benkert (1987) also listed many collections on *Bryum* sp. among the paratypes. As stated in the introduction, multiple unrelated hosts of a species often indicate unresolved taxa. The ascospores of collections from *C. purpureus* and from *Bryum dichotomum* are indeed very similar, and variations in ascospore size and ornamentation partly overlap. Nevertheless, our suspicion of hidden diversity is also supported by molecular data (Fig. 5, *L.* aff. *seaveri*), which indicate an independent taxon on *Bryum dichotomum*. Because of mostly scant collections on this host, description of *L.* aff. *seaveri* must be addressed in a later study. For the meantime, we recommend that only collections on *C. purpureus* be identified as *L. seaveri*.

Selected specimens examined—**AUSTRIA. Vienna, Central Cemetery**, host *Ceratodon purpureus*, 01.XII.2014 MV141201-02 (B 70 0010019). **GERMANY. Brandenburg, Potsdam**, slope along railway embankment at Berlin ring road near bridge across Caputher Chaussee, host *Ceratodon purpureus*, 23.XI1.986 DB (B 70 0010018, holotype). **Saxony-Anhalt, Galgenberg,** NE Elbingerode, host *Ceratodon purpureus*, 10.X.2015 GE (B 70 0100997). **Schleswig-Holstein, Appen,** host *Ceratodon purpureus*, 08.XI.2015 MV151108-01 (B 70 0100010). **Thuringia, S Wipperdorf,** 51.4463°N 10.6425°E, 240 m a.s.l., host *Bryum dichotomum*, 13.X.2017 JE51710 (B 70 0100993). **MONTENEGRO. Andrijevica Municipality, Štavna plateau,** 42.6988°N 19.6745°E, 1820 m a.s.l., between mosses on the edge of the pathway on mountain pasture, host *Ceratodon purpureus*, 18.VI.2017 LJ (PRC 4581).

Table 2. Comparison of main features of *Lamprospora* spp. with *seaveri*-type or similar spore ornamentation. (Measurements based on our observations, except for *L. funigera* and *L. irregulariata*.)

Lamprospora species	Apothecial diameter	Conspicuous fimbriate margin	Ascospores	Ornamentation	Host (moss family)
benkertii	0.4–1 mm	–	Globose, 13–16.5 µm	Main ridges 0.8–1.2 µm wide and high, forming a reticulum	*Trichostomum crispulum* (*Pottiaceae*)
ascoboloides	no data	–	Globose, 13–15 µm [12–14 µm in Benkert (1987)]	Ridges 1–2 µm wide, 1–1.5 high; often with blunt ends not forming a reticulum	cf. *Dicranella heteromalla* (*Dicranaceae*)
cailletii	1–2 mm	±	Globose, 15–16.5 µm	Ridges ≤0.8–1.5 µm wide & high, forming a reticulum; additional warts within the meshes of the reticulum	*Tortella tortuosa* (*Pottiaceae*)
dicranellae	1–3 mm	+	Globose, 15–16.5 µm	Ridges 1–2 µm wide & high, forming a rudimentary reticulum; numerous prominent warts	*Ditrichum heteromallum*, *D. pusillum* (*Ditrichaceae*)
funigera	1–3 mm	+	Globose, 12–13 µm	Fine ridges forming a reticulum	—
hispanica	1–2 mm	+	Subglobose, 16–19×15–18 µm, Q = 1.03–1.06	Main ridges 0.8–1.0 µm wide, 0.6–0.8 µm high, forming a dense reticulum	*Aloina aloides*, *A. ambigua* (*Pottiaceae*)
irregulariata	2–3 mm	–	Globose, 13–16 µm	Main ridges ca. 1 µm wide & high, forming an incomplete reticulum	—
leptodictya	0.8–1.8 mm	+	Subglobose, 15–17×13–15.5 µm, Q to 1.1	Ridges 0.5–0.9 µm wide, ≤0.5 µm high, not or rarely forming a reticulum	*Aongstroemia longipes* (*Dicranaceae*)
norvegica	0.7–1 mm	+	Slightly subglobose 13–14×12–13 µm, Q to 1.08	Ridges 0.3–0.7 µm wide, ≤0.5 high, forming a reticulum	*Ditrichum pusillum* (*Ditrichaceae*)
paechnatzii	1–2 mm	±	Globose, 14–16 µm	Ridges 0.3–0.8 µm wide & high, short & often S-shaped, rarely anastomosing, not forming a reticulum	*Bryum archangelicum* (*Bryaceae*)
seaveri	1–4 mm	+	Globose, 14–16 µm	Main ridges 0.3–0.8 µm wide & high, forming a reticulum, often with secondary reticulum	*Ceratodon purpureus* (*Ditrichaceae*)

The main features of the mentioned species are summarized in TABLE 2. To facilitate identification, we provide a new key.

Key to species of *Lamprospora* with *seaveri*-type (or similar) ascospore ornamentation

1. Hymenium yellow-white, apothecia 2–3 mm in diameter, little known species from India (possibly not belonging to *Lamprospora*) . . . ***L. irregulariata***
1. Hymenium shades of orange 2

2. Ascospores with main ridges 1–2 µm wide and many prominent warts between the ridges, host *Ditrichum* spp. . . . . ***L. dicranellae***
2. Ascospores with different ornamentation or host 3

3. Ascospores ornamented by often blunt ending ridges not or hardly forming a reticulum 4
3. Ascospores ornamented by anastomosing ridges forming a reticulum 6

4. Ridges of ascospore ornamentation strong, 1–2 µm wide, ascospores globose, 13–15(–17) µm, host probably *Dicranella heteromalla* . . . . ***L. ascoboloides***
4. Ridges of ascospore ornamentation weaker, 0.3–0.9 µm wide, a scospores globose or slightly subglobose 5

5. Ascospores mostly subglobose, 15–17 × 13–15.5 µm, host *Aongstroemia longipes*, in arctic–alpine habitats . . . . ***L. leptodictya***
5. Ascospores globose, 14–16 µm, host *Bryum archangelicum*, in the temperate zone . . . . ***L. paechnatzii***

6. Apothecia with conspicuous fimbriate margins, ascospores subglobose, 16–19(–22) × 15–18(–20) µm, host *Aloina* spp. . . . . ***L. hispanica***
6. Other combination of characters 7

7. Main ridges of ascospore ornamentation 1 µm wide or wider 8
7. Main ridges of ascospore ornamentation 0.3–0.8(–1) µm wide 9

8. Main ridges of ascospore ornamentation 0.8–1.5 µm wide with additional warts (difficult to observe), host *Tortella tortuosa* . . . . ***L. cailletii***
8. Main ridges of ascospore ornamentation about 1 µm wide often with a secondary reticulum within the meshes, host *Trichostomum crispulum*, southern-temperate distribution . . . . ***L. benkertii***

9. Apothecia ≤1 mm, ascospores often slightly subglobose, 13–14 × 12–13 µm, host *Ditrichum pusillum*, in arctic-alpine habitats . . . . ***L. norvegica***
9. Apothecia mostly >1 mm, host and habitat different 10

10. Ascospores globose, 12–13 µm, little known species from Australia, host unknown . . . . ***L. funigera***
10. Ascospores globose, 14–18 µm, host *Ceratodon purpureus* or *Bryum* spp. 11

11. Ascospores globose, 14–16 µm,
host *Ceratodon purpureus* . . . . *L. seaveri*

11. Ascospores globose or slightly subglobose, 14–18 µm,
host *Bryum* spp. . . . . *L.* aff. *seaveri*

There are several unpublished collections on different hosts with a *seaveri*-type ascospore ornamentation that cannot be ascertained as conspecific with any of the above-mentioned species. Because of these scant collections, no further details are provided here, but these unresolved specimens indicate a higher diversity in this group than previously thought.

Both morphological and molecular data confirm the very high host specificity of the bryophilous *Pezizales*. All evaluated species grow only on one particular moss species or on very closely related species as is the case with *L. hispanica* with hosts *Aloina aloides* and *A. ambigua*. In *L. seaveri*, which was reported from multiple hosts, the phylogenetic analysis clearly shows the presence of at least one other species on *Bryum dichotomum* (Fig. 5).

Although an identification of species can be undertaken by morphological characters only (Table 2), differences between species are sometimes subtle and variations of some features can overlap. The easiest way to differentiate between species is to consider the ecology and host identity. Specimens from hitherto unknown hosts, or with ascospores differing from those of known species on a particular host, are likely candidates for new species.

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